



Behavioral Lateralization in the Florida Manatee (*Trichechus manatus latirostris*)

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We examined side preferences in the Florida manatee (*Trichechus manatus latirostris*) through observations of limb use (right and left flipper) in 123 wild and 16 captive individuals. We also analyzed archival data, the United States Geological Survey Sirenia Project Manatee Individual Photo-identification System dataset, to determine lateralization of evasive action from boats. Wild and captive manatees displayed flipper lateralization at the individual, but not the population level for several behaviors including substrate touches, sculling, and feeding. In contrast, manatees were lateralized at the population level for boat-scar biases, with more manatees showing a left scar bias (45.3%) versus right (34.3%) or dorsal/ambipreferent (20.3%).

Two manatees at Mote Marine Laboratory, participating in a two-choice tactile discrimination task, each investigated the left target first rather than the right target 100% of the time over hundreds of trials (Bauer et al., 2012). Although this action might be explained as an inadvertent training effect, it also suggested possible lateralization of behavior. Many animals display lateralization, in which the two hemispheres of the brain are specialized for different functions reflected in behavior (Vallortigara, Rogers, & Bisazza, 1999). Population-level lateralization occurs when a majority of the population of a species exhibits the same lateral preference. Individual-level lateralization occurs when individual animals show clear lateral preferences, but the side preferences are divided approximately equally within the population. Behavioral side preferences at both the population and individual level are indicative of lateralization of the brain.

A putative advantage of lateralization is enhanced neural efficiency. If a behavior is controlled by one hemisphere, the other hemisphere is freed for other tasks. It also might reduce interference between hemispheres in controlling unilateral behavior (Rogers, 2002).

Observing behavioral preferences in diverse contexts and tasks can reveal the specializations of each hemisphere. In a review of the literature on behavioral lateralization, Rogers (2002) reported that in a majority of the species studied, the left hemisphere is responsible for inhibiting responses (such as escape), focused attention, sequential analysis, inhibiting the right hemisphere, feeding, and prey capture. The right hemisphere, however, appears responsible for rapid responses, unfocused attention, intense emotions, parallel processing, spatial information (e.g., cognitive maps), and species-typical responses such as escape, fear, and aggression.

Lateral preferences can be observed in motor tasks, where each hand or limb preferentially performs a different type of task. In the case of humans, the dominant hand preferentially grasps objects, while the other provides stabilization (Stone, Bryant, & Gonzalez, 2013). Similarly, this specialization has been found in non-human primates as well. For example, Hopkins, Bennett, Bales, Lee, and Ward (1993) found that bonobos

(*Pan paniscus*) displayed a left lateral bias for carrying, and a right lateral bias in leading limb as well as for feeding while holding food with the left hand. In addition, hand preference has been reported to depend on posture, where certain postures reveal no hand preference, but in situations where the non-dominant hand was required for support, laterality was observed more clearly (Hashimoto, Yamazaki, & Iriki, 2013). This suggests that not all tasks will be performed preferentially with the dominant hand, but that specializations for each side exist, providing evidence for differential lateralization.

Fagot and Vauclair (1991) developed task complexity theory to explain specializations of limb preference in a variety of species. They proposed that tasks requiring more physical skill or manipulation should demonstrate a strong lateral bias, while comparatively simple tasks should not elicit lateralized behavior. Task complexity theory suggested that more cognitively complex tasks and tasks requiring bimanual coordination would be likely to reveal a population-level lateral preference. Several studies of chimpanzees' (*Pan troglodytes*) manual actions provided support for this theory (Chapelain, Bec, & Blois-Heulin, 2006; Hopkins, 2006; Vauclair, Meguerditchian, & Hopkins, 2005). These studies provide a platform on which to base observation categories and expectations for investigating lateralization in the Florida manatee (*Trichechus manatus latirostris*).

Although much of the handedness and lateralization research has focused on primates, these are not the only non-human animals to exhibit lateralization in complex tasks. Asian elephants (*Elephas maximus*), the closest living terrestrial relative of the Florida manatee, displayed strong individual-level lateral biases for trunk movements during grass feeding (Martin & Niemitz, 2003). Furthermore, elephants demonstrate stronger lateral preferences for the more complex task of trunk manipulation during feeding than during simple reaching.

Many species of marine mammals apparently display behavioral lateralization at the population level in locomotion, feeding behaviors, and eye use, although small sample sizes in some cases, as well as differences in direction of lateralization between tasks in some studies, suggest a need for further research. These preferences include population-level turning and eye preferences in bottlenose dolphins (*Tursiops truncatus*; Ridgway, 1986; Sobel, Supin, & Myslobodsky, 1994), individual-level turning preferences in California sea lions (*Zalophus californianus californianus*; Wells, Irwin, & Hepper, 2006), and turning preferences in beluga whales (*Delphinapterus leucas*; Marino & Stowe, 1997). Fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sei (*Balaenoptera borealis*), and Bryde's (*Balaenoptera edeni*) whales display lateral lunge asymmetries (Tershy, 1992), and humpback whales (*Megaptera novaeangliae*) display lateral biases in turns to one side during bottom feeding and flipper slapping (Clapham, Leimkuhler, Gray, & Mattila, 1995). Walrus (*Odobenus rosmarus*; Levermann, Galatious, Ehlme, Rysgaard, & Born, 2003) and Indo-pacific bottlenose dolphins (*Tursiops aduncus*; Sakai, Hishii, Takeda, & Kohshima, 2006) display marked flipper preferences. Bottlenose dolphins also show performance asymmetries and preferences for one eye over the other in many tasks in both the wild and in captivity (Delfour & Marten, 2006; Kilian, Von Fersen, & Güntürkün, 2000, 2005; Sakai et al., 2006; Yaman, Von Fersen, Dehnhardt, & Güntürkün, 2003), although the eye preference appears to be different for different tasks (e.g., social vs. object discrimination).

Lateralization has not been reported in manatees to our knowledge. Manatees use their flexible flippers in a variety of ways that lend themselves to laterality analysis including manipulating food (Hartman, 1979; Marshall, Huth, Edmonds, Halin, & Reep, 1998; Marshall et al., 2003), locomotion along the substrate, sculling, and pushing off the substrate (Marsh, O'Shea, & Reynolds, 2011; Reep & Bonde, 2006).

Another approach to understanding laterality in these animals is provided by the distribution of boat scars so commonly found in Florida manatees. These conspicuous scars may be easily utilized as a measure of

lateralization for evasive behavior. Previous studies indicate that manatees do attempt to avoid boats by moving into deeper water and increasing swimming speed (Nowacek et al., 2004) or by diving (Wright, Ackerman, Bonde, Beck, & Banowetz, 1995). However, these studies have not addressed the egocentric directionality of these evasions. To the best of our knowledge, no one has investigated whether manatees tend to turn to their left or their right while evading a boat.

Many other animals exhibit lateralized evasion responses at the population level, including numerous species of fish (Cantalupo, Bisazza, & Vallortigara, 1995; De Santi, Sovrano, Bisazza, & Vallortigara, 2001; Facchin, Bisazza, & Vallortigara, 1999) and toads (*Bufo bufo*, *Bufo viridis*, *Bufo marinus*; Lippolis, Bisazza, Rogers, & Vallortigara, 2002). Sheep (*Ovis aries*) avoid objects by turning to the right (Versace, Morgante, Pulina, & Vallortigara, 2007). Analysis of scarring has also been used as a successful method to reveal population-level behavioral lateralization in trilobites (*Trilobita*; Babcock, 1993), whitefish (*Coregonus nasus*, *Coregonus clupeaformis*; Reist, Bodaly, Fudge, Cash, & Stevens, 1987), impalas (*Aepyceros melampus*; Jarman, 1972), and humpback whales (Clapham et al., 1995).

We examined flipper uses in manatees for evidence of behavioral lateralization at the population and individual level. We also investigated the uniformity of preferences across tasks for evidence of task specificity and evaluated the consistency of preferences over time. Based on the results of the literature suggesting that task complexity affects preferences, we expected manatees to display stronger side preferences for manipulatory and bimanual actions, including feeding and escape behaviors, than for ostensibly simpler behaviors such as sculling, substrate touches, and touching other manatees. The study included both wild and captive manatees. We also used a large dataset of boat scar descriptions from manatees in Crystal River, Florida to analyze lateralization of evasion behavior in manatees.

Method

Subjects

Field observations were made near the Three Sisters Springs sanctuary area of Crystal River on the west coast of Florida. The observation period lasted from January 6 through January 28, 2008. Overall, 123 different wild manatees and 16 healthy, captive manatees were observed.

Age class and sex could not be determined for all wild manatees; however, this information was available for the captive manatees. Eleven male and five female manatees were observed in captivity ranging from calves to adults. Thirteen of the captive manatees had been injured or orphaned and were brought into captivity for temporary rehabilitation before release at a later date.

Captive Facilities

The captive manatees were housed in four different Florida locations: Lowry Park Zoo in Tampa; Mote Marine Laboratory and Aquarium in Sarasota; Parker Manatee Aquarium in Bradenton; and The Seas at Epcot, Walt Disney World, Lake Buena Vista, FL. Lowry Park Zoo and Mote Marine Aquarium were outdoor facilities. Parker Aquarium and The Seas were indoor habitats (Table 1).

Table 1
Demographic Characteristics of Captive Manatees

Name	Age Class	Sex	Location	Environment	Volume (in Ls)	Max Depth (in m)
Baron	Subadult	Male	Lowry	Outdoor	473,176	3.05 - 3.66
Beach Boy	Subadult	Male	Lowry	Outdoor	473,176	3.05 - 3.66
Bock	Adult	Male	Seas	Indoor	465,605	3.27
Buffett	Adult	Male	Mote	Outdoor	264,979	3.05
Coral	Subadult	Female	Parker	Indoor	227,125	3.05
Corallee	Calf	Female	Parker	Indoor	227,125	3.05
Gene	Adult	Male	Lowry	Outdoor	473,176	3.05 - 3.66
Hugh	Adult	Male	Mote	Outdoor	264,979	3.05
Hurricane Bay	Adult	Male	Lowry	Outdoor	473,176	3.05 - 3.66
Hurricane	Adult	Male	Lowry	Outdoor	473,176	3.05 - 3.66
Jackie	Adult	Female	Lowry	Outdoor	473,176	3.05 - 3.66
LilNap	Calf	Male	Parker	Indoor	227,125	3.05
Lou	Adult	Male	Seas	Indoor	465,605	3.27
Baby Sister	Subadult	Female	Parker	Indoor	227,125	3.05
Snooty	Adult	Male	Parker	Indoor	227,125	3.05
Whitaker	Subadult	Female	Parker	Indoor	227,125	3.05

Note. Lowry = Lowry Park Zoo, Tampa, FL; Mote = Mote Marine Aquarium, Sarasota, FL; Parker = Parker Manatee Aquarium, Bradenton, FL; Seas = The Seas at Epcot®, Walt Disney World® Resorts, Lake Buena Vista, FL.

Procedure

Wild observations. Each manatee was observed for 10-30 min or until it swam too far away for the researchers to follow. Observations by two observers were made between the hours of 8:00 a.m. and 4:00 p.m. Actions were recorded on a waterproof dive board and later entered into a computer data base. Actions were only recorded if the researcher could see the manatee's head and both pectoral flippers simultaneously. Each researcher first wrote or drew a description of the notable physical characteristics of the manatee that was being observed (scars, barnacles, algae, etc.) and, if possible, the sex and general age of the manatee (calf, subadult, adult).

The actions observed in the wild were sculling, substrate touches, body touches, digging in the substrate, touching other manatees, as well as grabbing of ropes, tourists, and boats (see Appendix for definitions). In captivity, other behaviors were recorded in addition to those observed in wild manatees: feeding, pulling out of the water, and interacting with enrichment devices, although the latter behaviors were infrequently observed.

Continuous actions were recorded as frequencies of individual behaviors rather than bouts of behavior. For example, each sculling action was counted as separate if it consisted of one entire circle of the flipper. Other actions were recorded separately if an interval of several seconds occurred between the actions, or if a new action began. In a few cases, individual wild manatees were observed more than once on different days. In these cases, the observations from all days were combined to calculate the total observations for that manatee.

Captive observations. Observations were made during two different periods, 2005-2006 and 2008-2009. All observations were made in the morning through underwater viewing windows. Most observations started before facilities opened to the public, although they often continued into visitor hours.

The same information was recorded for captive manatees as was recorded for the wild manatees. The actions, flipper used, number of flipper uses, and, in some cases, manipulated object were recorded. Each manatee was observed in 30-min sessions until at least 100 unilateral flipper uses were recorded, with one exception (Hurricane Bay, who was observed over multiple sessions, displayed only 81 unilateral flipper uses and 16 bilateral uses). Focal sampling with continuous recording methods was used for determining frequency and type of lateralized behavior.

Four of the captive manatees were observed at a later date to test for the consistency of preferences across time and also to test for reliability of the preference scores across time and observers. Three manatees were observed four years later and by a different

observer on each occasion, and one manatee was observed one month later by the same observer. All four manatees displayed the same overall side preferences as indicated by their Handedness Index (HI) scores during the second observation period, supporting the stability of lateral preferences over time ($r = 0.85$).

Data Analysis

Flipper preferences. Flipper preferences were analysed in several steps. First, the preferences for left or right flipper were determined by using HI scores supplemented with a z-score analysis. The HI were then used to select a sample minimally affected by number of subjects by correlating HI with N . Finally, chi-square analyses were performed on the remaining sample to determine statistically significant lateral preferences.

For each manatee, a HI score was calculated by subtracting the number of left-limb responses from the number of right-limb responses and dividing that number by the total unilateral flipper responses (Hopkins et al., 2005). Handedness Index scores range from -1.0 to 1.0, where negative scores represent a left-limb bias and positive scores represent a right-limb bias. The absolute value of the score represents the strength of the preference. Hopkins et al. interpreted the absolute values of the HI as follows: 0.0-0.09 represents no bias; 0.1-0.49 represents a weak bias; 0.5-1.0 represents a strong bias. An overall HI score was calculated for each manatee along with a separate HI score for each activity. All tests were two-tailed with an alpha level of 0.05.

In addition, a z-score was calculated from the number of right flipper behaviors and the total number of behaviors. Scores of one standard deviation or more were considered lateralized such that scores less than or equal to -1.96 were considered strongly left lateralized, -1.96 to -1 were considered weakly left lateralized, -1 to 1 were considered ambipreferent, 1 to 1.96 were considered weakly right lateralized, and values greater than 1.96 were considered strongly right preferent (Hopkins, 2006).

Scars from boat strikes. Data were taken from the United States Geological Survey Sirenia Project (USGS) Manatee Individual Photo-identification System (MIPS), which records identifying features of manatees, including scars. The data were screened by Cathy Beck, a USGS field biologist skilled in photographic analysis, to eliminate instances that were not clearly attributable to boat strikes. Although there may be ambiguity in the source of a few of the scars, the substantial majority were associated with boat strikes. The dataset contained 1,907 descriptions of scars from boat collisions on 408 manatees observed through the year 2009 in Crystal River. The scars were classified based on many characteristics, including on which side of the body the scars occurred: left, right, or dorsal (defined as a scar crossing the midline). Scars were also characterized based on how many marks occurred in each scar. For example, a single propeller scar event might contain numerous separate strikes resulting from the same event. We analyzed the distribution of scars using the number of separate scar events on each side by calculating a scar bias index for each manatee. The total number of scar events was calculated simply by ascribing the number 1 for each right scar event, 0 for dorsal events, and -1 for left scar events. The numbers for each manatee were added and the resulting quantity determined *scar bias*, with a positive number denoting a right bias, 0 denoting no bias or dorsal, and a negative number denoting a left bias.

Results

The absolute values of the HI scores were negatively correlated with the total number of unilateral flipper uses when all (wild and captive) subjects were used, $r(139) = -0.26$, $p = 0.002$. In other words, the fewer observations of unilateral flipper behavior that were made on any one individual, the more likely they were to be identified as lateralized, which is clearly a spurious effect arising from a small number of observations. When the number of individuals in the sample was limited to those with 20 or more observations, the correlation disappeared. For this reason the minimum number of unilateral flipper observations necessary for a subject to be kept for analysis for lateral preferences in overall behaviors combined and for any individual behavior, as well, was 20.

Of the 123 wild manatees observed, only 52 manatees met these criteria for flipper preference. All 16 captive manatees were included, as more than 81 unilateral flipper uses were observed for each subject. The overall category combined the flipper uses for all behaviors to generate a HI score. In the case of each separate behavior category, a subset of the subjects selected in the overall category, all unilateral flipper uses had to be of the same behavior. The same criteria were used to determine whether a captive manatee was included in

each separate behavior analysis: a minimum of 20 unilateral flipper uses for that behavior alone. The final total of wild and captive manatees in the sample was 68.

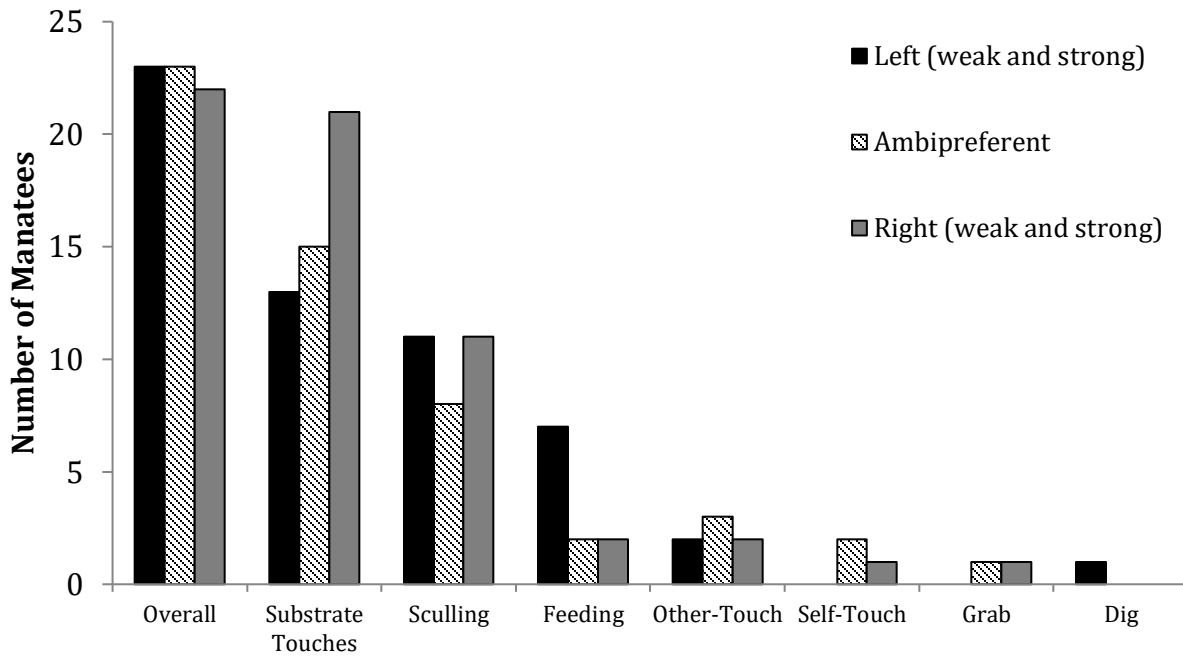


Figure 1. Number of manatees displaying each flipper preference across the different behaviors for all manatees. Left and right flipper preferences combine weak and strong preferences.

The wild and captive manatee populations did not display different overall preferences as indicated by HI scores, $t(66) = 0.38, p = 0.703$ (Figures 1, 2, and 3). The differences between the two populations for the substrate touching and sculling also revealed that the populations did not differ significantly, $t(47) = 0.97, p = 0.351$ and $t(28) = 1.26, p = 0.218$, respectively, so the groups were combined for the remaining analyses. In addition, age class was not associated with laterality, $F(2, 65) = 1.47, p = 0.236$. Although a significant effect for sex was found among those manatees where sex could be determined, $t(42) = 2.24, p = 0.030$, the handedness index scores fell primarily in the no bias range, male $M = -0.07$, female $M = 0.10$ (Hopkins, 2006), which suggests a difference of little practical significance.



Figure 2. Number of individual wild manatees displaying each flipper preference across behaviors. Left and right flipper preferences combine weak and strong preferences.

Of the 68 overall cases analysed, 15 were strongly left lateralized ($z \leq -1.96$), 8 were weakly left lateralized (z between -1.95 and -1), 23 were ambipreferent (z between -0.99 and 0.99), 11 were weakly right lateralized (z between 1 and 1.95), and 11 were strongly right lateralized ($z \geq 1.96$; Figure 4).

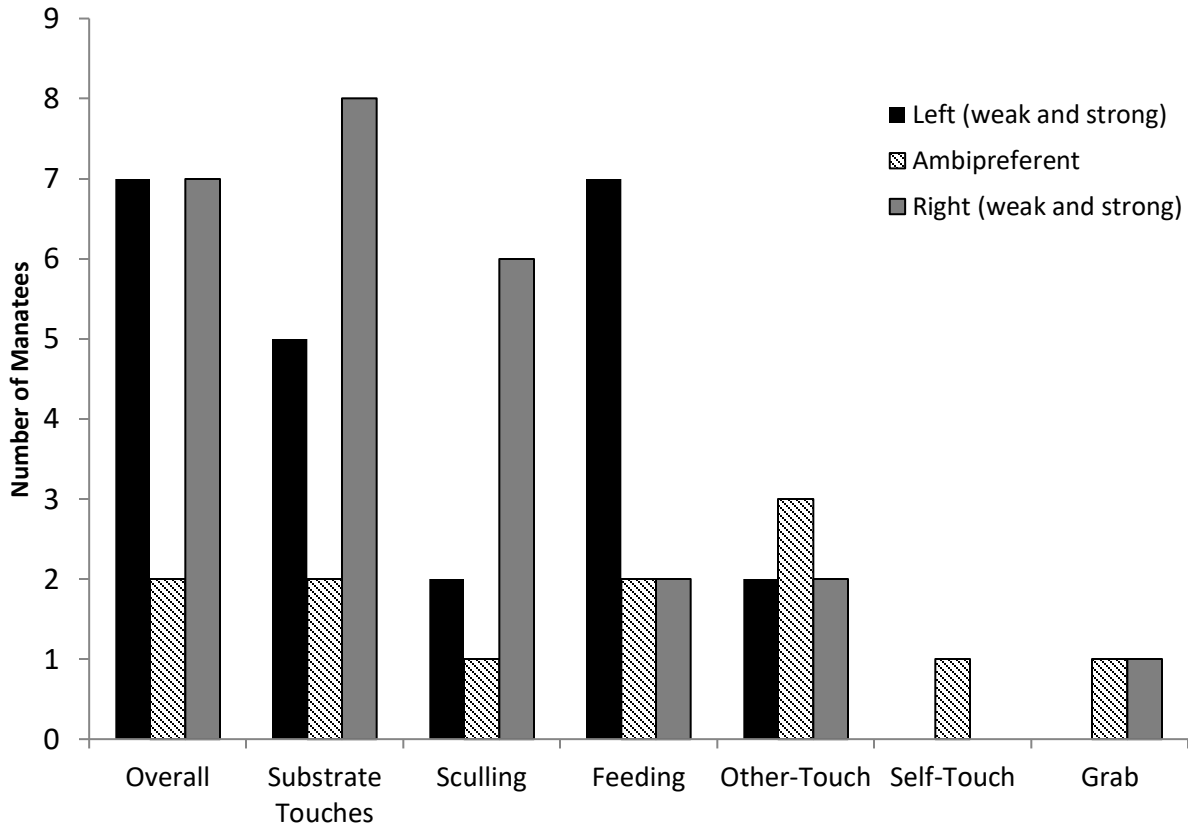


Figure 3. Number of captive manatees displaying each flipper preference across tasks. Left and right flipper preferences combine weak and strong preferences.

Population level lateral preferences were identified when left or right behaviors differed significantly in a three-condition comparison (left, right, and ambipreferent). Lateralization at the individual level was determined in two-condition analysis (left or right vs. ambipreferent). The overall side preferences did not differ, suggesting that there was no laterality at the population level for flipper use. A comparison of individual flipper preference vs. no flipper preference, however, showed that there were significantly more lateralized individuals than not, $\chi^2(1, N = 68) = 7.12, p = 0.008, \phi = 0.32$, but there was no difference in frequency between left-preference and right-preference, indicating that each side preference was equally frequent in the sample (Figure 1).

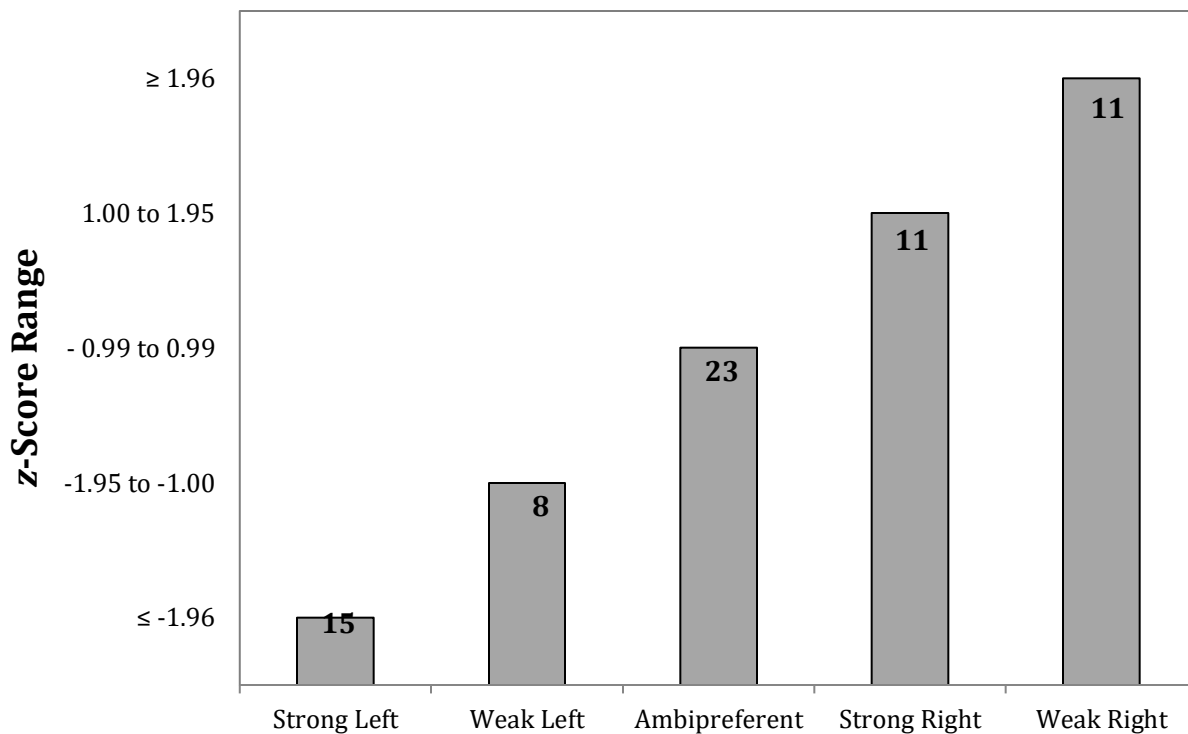


Figure 4. Bars show the z-score range that determines the lateralization categories. The numbers inside the bars indicate the number of manatees in each category.

Population preferences (left, right, or ambipreferent) for the separate behaviors did not differ significantly from chance when left, right and ambipreferent were compared. When comparing preference versus no preference (left or right vs. ambipreferent) in flipper use for sculling, subjects showed a significant preference, $\chi^2(1, N = 30) = 8.53, p = 0.003, \phi = 0.53$, but this preference was equally frequent for either side. In other words, there was an individual lateral preference for flipper use, not represented at the population level. Similarly, for substrate touches, individual subjects showed a consistent side preference, $\chi^2(1, N = 49) = 12.76, p < 0.001, \phi = 0.51$, but this preference was equally frequent for each side. The distribution of flipper use in feeding behavior (Figure 1) suggests a left preference at the population level, but the small expected frequencies for some comparisons precluded an appropriate chi-square analysis. An analysis of preference vs. no preference indicated that feeding was lateralized, $\chi^2(1, N = 11) = 4.45, p < 0.050, \phi = 0.64$, at the individual level.

Fagot and Vauclair (1991) report that lateral preferences might change consistently among tasks (e.g., use of the dominant flipper for more complex tasks and the non-dominant flipper for simpler, balance-based tasks). To test for this possibility, left flipper preference was counted as right flipper preference and vice versa for two behaviors, substrate touches and sculling. Tests with lateral preferences for these tasks inverted did not provide different results for overall lateralization. For this reason, all results reflect direct observation values (i.e., left preference considered a sign of left dominance and right preference considered a sign of right dominance).

For analysis of scar data, dorsal scars and ambipreferent responses (equal number of scar events on each side) were combined since they both indicate a lack of lateral bias. The distribution of scar biases differed significantly from a distribution expected by chance, $\chi^2(2, N = 408) = 38.43, p < 0.001, \phi = 0.31$, with more manatees exhibiting a left than a right scar bias (Figure 5). A similar pattern emerged when taking into account the total number of scar marks for each event, $\chi^2(2, N = 408) = 86.88, p < 0.001, \phi = 0.46$.

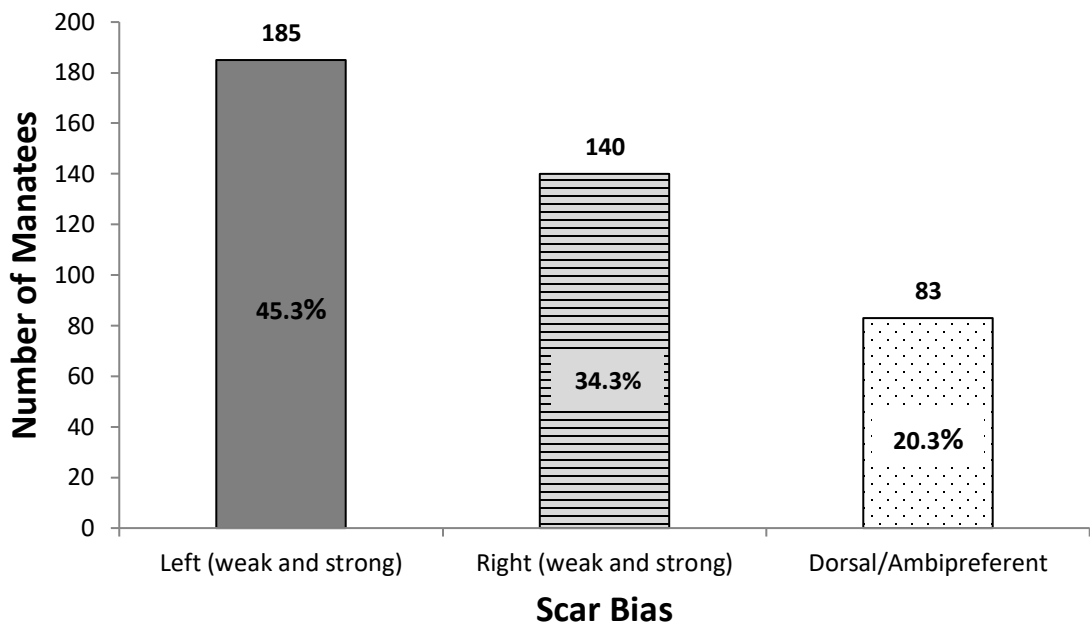


Figure 5. Numbers above the bars indicate the number of manatees. The numbers inside the bars indicate the percentage of manatees displaying each bias. Dorsal and ambipreferent scars were combined.

Discussion

Three substantive findings on manatee laterality are reported:

- Scars from boat strikes on manatees were over-represented on the left-side of their bodies, which represents population-level laterality.
- Several flipper behaviors indicated individual-level laterality but no population level preference.
- The pattern of some behaviors such as feeding suggested possible laterality at the population level, but sample sizes were too small for meaningful inferential analysis.

The left boat-scar bias indicated a biased body orientation with respect to approaching boats, but since the direction of approach and orientation of the manatees before the strikes were unknown, we do not know the topography of the responses and the corresponding hemispheric specializations. Manatees did not exhibit a population-level bias for flipper behaviors, but they did exhibit individual-level preferences (for substrate touches, sculling, and feeding). Although we did not expect manatees to display strong individual lateral preferences—as these are more likely to occur for more difficult, manipulatory activities (cf. Martin & Niemitz, 2003)—the lateralized activities that the manatees performed most often during observation were

seemingly simple, non-manipulatory activities such as sculling and substrate walking. The manatee preferences were nevertheless robust, with phi coefficients (measures of effect size) all exceeding 0.50.

A comparison of flipper use in feeding behavior with substrate touching, a complex versus a more simple behavior, suggests that task complexity (e.g., Chapelain et al., 2006; Fagot & Vauclair, 1991; Hopkins, 2006; Vauclair et al., 2005) may not differentiate among lateralized behaviors in manatees, but the small sample for feeding suggests that conclusions be deferred until larger sample sizes are obtained. Feeding, grasping, digging, and touching—behaviors observed infrequently—represent a subset of the social and exploratory behaviors that might allow clearer differentiation of complex and simple behaviors in future studies.

Furthermore, a more detailed analysis of simultaneously occurring behaviors might elucidate task complexity. Vallortigara and colleagues (1999) discussed how preferences for differential lateralization may be the result of multitasking. For example, if one flipper were preferred or specialized for certain tasks, the other flipper would be free to perform other behaviors at the same time. For example, a manatee could use one flipper to walk along the substrate or swim, while the other was used to bring food to the mouth, a combination we did not record in this study. Both wild and captive manatees displayed a preference for walking along the substrate with one flipper. A preference for one flipper while walking along the bottom may leave the other flipper free to specialize in other tasks similar to Campbell's monkeys using the left hand to hold objects while the right hand was free to perform a main action (Chapelain et al., 2006). Furthermore, strong biases shown in studies of manatees in a two alternative texture discriminations, a 100% left bias for two manatees reported by Bauer and colleagues (2012) and a strong right bias reported by Bachteler and Dehnhardt (1999), suggest that research should also target laterality of facial movement and turning behavior.

Manatees exhibit population-level and individual-level lateralization, the former as suggested by the location of boat scars and the latter by various flipper behaviors in both wild and captive manatees. These results indicate hemispheric lateralization of the Florida manatee brain. In the future, more detailed investigations of this lateralization emphasizing complexity and function of the lateralized behaviors, will allow us to better explain the brain-behavior relationships in manatees.

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Appendix

Behavior Definitions

Digging. Manatee excavates the substrate

Feeding. Manatee uses flipper to push food toward or into mouth

Grab. Manatee uses flipper to clutch objects

Sculling. Flipper makes of full circle rotation to move the manatee through the water touching only water

Other touch. Manatee makes flipper contact with another manatee

Self-touch. Manatee makes flipper contact with its own body

Substrate touch. Manatee pushes off or pulls body along the substrate.

Submitted: August 15th, 2016

Resubmitted: October 7th, 2016

Accepted: October 11th, 2016